Electrophysiological correlates of the somatotopically organized tactile duration aftereffect

Baolin Li [a], Jianrong Jia [b], Lihan Chen [c,d,*], Fang Fang [c,d,e,f,*]

[a] *School of Psychology, Shaanxi Normal University, Xi'an 710062, China*
[b] *Institute of Psychological Sciences, Hangzhou Normal University, Hangzhou 311121, China*
[c] *School of Psychological and Cognitive Sciences and Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing 100871, China*
[d] *Key Laboratory of Machine Perception (Ministry of Education), Peking University, Beijing 100871, China*
[e] *Peking-Tsinghua Center for Life Sciences, Peking University, Beijing 100871, China*
[f] *PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing 100871, China*

ARTICLE INFO

ABSTRACT

Adaptation to sensory events of long or short duration leads to a negative aftereffect, in which a new target event (of median duration) following the adaptation will be perceived to be shorter or longer than is actually the case. This illusion has been observed in visual, auditory, and tactile modalities. This study used event-related potentials (ERPs) to examine the tactile duration aftereffect, using the contingent negative variation (CNV) and the late positive component (LPC) as a way to characterize the temporal processes. The tactile duration adaptation was found to induce a significant aftereffect within a somatotopic framework. Moreover, the CNV in the contralateral scalp and the LPC in the fronto-central scalp were both modulated by the tactile duration adaptation. Specifically, adaptation to a short tactile duration increased the CNV and LPC amplitudes, whereas adaptation to a long tactile duration decreased them. This modulation was contingent on the topographic distance between fingers, which was only observed when the adapting and test fingers were consistent or adjacent, but not homologous. In sum, these results reveal a coherent behavioral-electrophysiological link in the somatotopically organized tactile duration aftereffect.

1. Introduction

Our brain adapts to temporal information to maintain a coherent representation of the world (Burr et al., 2007; Fujisaki et al., 2004; Johnston et al., 2006); one such example is the well-documented phenomenon of duration adaptation (Heron et al., 2012; Li et al., 2015; Walker et al., 1981). In duration adaptation, the perceived duration of a subsequent event (of medium physical duration) is biased by repetitive exposure to a relatively short or long sensory stimulus. This duration aftereffect hence supports the hypothesis of "duration channels" (Heron et al., 2012).

Whereas the duration adaptation has been extensively studied in audition and vision, whether the somatosensory system can similarly adapt to changes in duration remains largely unknown. To address this, we recently conducted several behavioral experiments involving tactile duration adaptation (Li et al., 2019). In this study, participants were first adapted to a long (640 ms) or short (160 ms) duration tactile stimulus,

and then completed different temporal tasks such as duration discrimination and reproduction. The results showed that adaptation to a relatively long tactile duration shortened the perceived duration of subsequent tactile stimuli, while adaptation to a relatively short tactile duration lengthened them. Moreover, the tactile duration aftereffect is modality specific, tuned around the adapting duration, and dependent on the topographic distance between fingers – in other words, it is a robust duration adaptation mechanism in the somatosensory system. The behavioral findings indicated the modality-specific timing mechanisms, and revealed that early somatosensory areas play an essential role in the perception of sub-second tactile duration. However, little is known about the temporal dynamics of the duration aftereffect.

In the channel-based model, duration information is encoded and mediated by duration-selective channels, with "channel-based" analysis predicted by the duration-tuned neurons in the brain (Heron et al., 2012). Adaptation to a duration selectively diminishes the responses of relevant channels, thus modifying the subsequent temporal encoding of

these duration channels and resulting in the duration aftereffect. Consistent with this hypothesis, a previous study has demonstrated that the visual duration adaptation modulates subsequent temporal encoding (Li et al., 2017). However, duration perception involves a series of temporal information processing, including the earlier encoding as well as later stages such as temporal memory storage and decision-making (Gibbon, 1977; Treisman, 1963). In this information processing perspective, whether and how the tactile duration adaptation affects subsequent temporal encoding or later stages in the process (e.g., temporal memory) is far from clear. Given the behavioral characteristics of the tactile duration aftereffect (Li et al., 2019), by using electrophysiological recording with electroencephalography (EEG), we predicted that the effect of sub-second tactile duration adaptation should operate on modality-specific mechanisms (specific to tactile modality) and reveal the distributed aspects of temporal information processing across differential but featured stages (Murai et al., 2016).

Among EEG measures, the contingent negative variation (CNV) is particularly implicated in cognitive processes associated with time-keeping. The CNV is a slow negative-going wave mainly elicited in the fronto-central scalp and unfolds as a duration is being processed. Previous studies have extensively investigated the role of the CNV in temporal processing in different modalities, including the tactile modality (Macar and Vidal, 2003; Nagai et al., 2004; Pfeuty et al., 2003). Despite existing debates on the perceptual and cognitive functions of the CNV, studies have found that CNV amplitude reflects the perceived duration of a stimulus (Bendixen et al., 2005; Macar et al., 1999; Wiener et al., 2012). Larger amplitudes are associated with perceived longer passages of time. Hence, the CNV has been described as an "online index of timing" (Macar and Vidal, 2004; Ng and Penney, 2014). As such, this mechanism provides a means to investigate the neural correlations of temporal illusions. For example, previous studies have demonstrated that the visual duration adaptation (Li et al., 2017), but not flicker-induced time dilation (Herbst et al., 2014), modulates the temporal encoding indexed by the CNV amplitude.

Event-related potential (ERP) components that develop after the presentation of a stimulus are also involved in temporal processing (Kononowicz and van Rijn, 2014; Lindbergh and Kieffaber, 2013; Paul et al., 2003, 2011; Tarantino et al., 2010). For example, Kononowicz and van Rijn (2014) demonstrated that the amplitude of N1P2 components evoked by a sound terminating a comparison interval was a better predictor of subjective duration than the preceding CNV; this also suggests that timing processes continue after CNV resolution. Moreover, certain post-stimulus positive components have been proven to be related to later stages of time processing. For example, the time-related late positive component (LPCt) is associated with temporal decision making (Paul et al., 2003, 2011). In addition, it has been suggested that P150, appearing after the offset of the comparison interval, is involved in working memory processes (Tarantino et al., 2010).

Here, we hypothesize that the CNV and post-stimulus components can be used to probe the tactile duration aftereffect, and to further examine how that adaptation modulates subsequent tactile temporal processing. Previously we found that the visual duration adaptation modulates subsequent visual temporal encoding (Li et al., 2017). Thus, we expected to find a similar tactile duration adaptation effect on subsequent temporal encoding indexed by CNV amplitude. Specifically, we hypothesized that the CNV amplitude would become larger after adaptation to a relatively short tactile duration and vice versa, and would change as a function of the topological distance between adapting and test fingers (Li et al., 2019). For the presumed post-stimulus component, we mainly focused on its role during the temporal memory. We aimed to reveal a duration adaptation effect on the post-stimulus component.

In the present study, we implemented a typical duration adaptation experimental paradigm that includes two phases within an experiment (Fig. 1). During the adaptation phase, participants were adapted to a tactile stimulus presented on a fingertip of the index, middle, or contralateral index finger. The stimulus had a relatively long (800 ms) or short (200 ms) duration. In the test phase, a tactile test stimulus of median duration (500 ms) was presented on the fingertip of the index finger. Participants performed a temporal discrimination task to judge whether the tactile test duration was longer or shorter than the visual reference duration. We found that tactile duration adaptation induced a significant "negative" duration aftereffect when the adapting and test fingers were consistent or adjacent, but not when they were homologous. CNV amplitude in the contralateral scalp and late positive component (LPC) amplitude in the fronto-central scalp were measured to characterize the duration adaptation effects on the earlier temporal encoding and subsequent temporal memory processes. Crucially, these signatures were contingent on the topographic distance between fingers, consistent with the behavioral findings.

2. Results

2.1. Behavioral results

To examine the tactile duration aftereffect, the point of subjective equality (PSE) was calculated for each condition, for each participant.
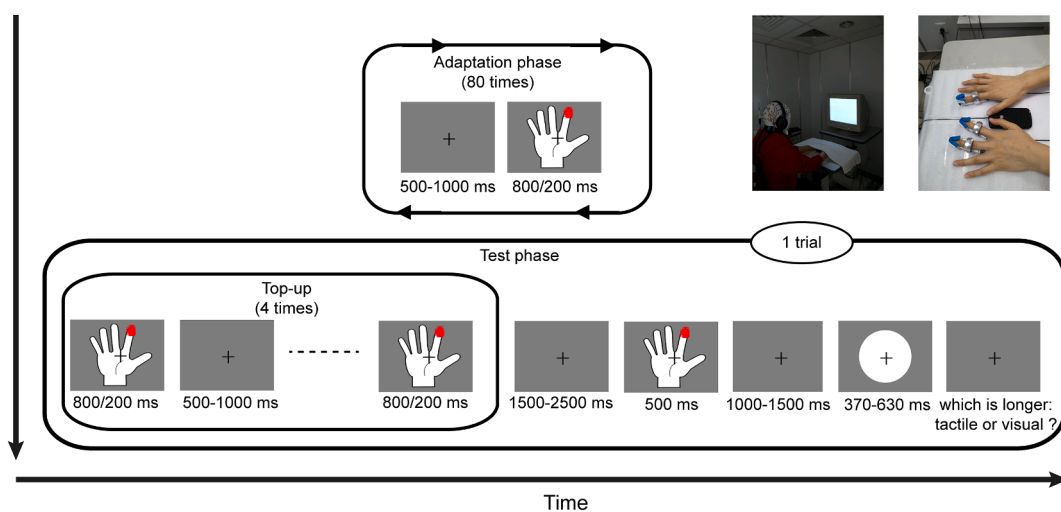
Fig. 1. Schematic representation of an adaptation block in the consistent condition. Each adaptation block had two phases: adaptation and test. The adapting stimulus with a fixed duration was repeatedly presented on a fixed fingertip during the adaptation phase and during the top-up period of the test phase. A tactile test and a visual reference were then presented successively. Participants were asked to judge whether the tactile or visual stimulus was of longer duration.

The PSE was calculated by fitting a psychometric function using logistic regression (50% response level on the psychometric function, Fig. 2A). For each subject, the PSE value for the no-adaptation condition was subtracted as a baseline (BA) from PSE values in the adaptation conditions respectively [i.e., adapt to a short duration on the consistent (CS), homologous (HS), and adjacent (AS) fingers; adapt to a long duration on the consistent (CL), homologous (HL), and adjacent (AL) fingers; see also the Procedure section]. These differences were defined as aftereffect magnitudes (AMs) for different adaptation conditions (Fig. 2B). The resulting AMs were positive when the adaptation measure was greater than the baseline measure, suggesting that the tactile duration adaptation expanded the perceived duration of subsequent tactile stimuli. In contrast, negative AMs indicated that the perceived tactile duration was contracted by the adaptation. AMs were analyzed with the repeated-measures ANOVA. The Greenhouse-Geiser correction was applied considering violation of sphericity assumption.

A 2 (adapting duration: short, long) × 3 (adapting location: consistent, adjacent, homologous) repeated-measures ANOVA was implemented. The main effect of the adapting duration was significant ($F(1, 17) = 29.843$, $p < 0.001$, $\eta^2 = 0.335$), the main effect of the adapting location was marginally significant ($F(2, 34) = 2.904$, $p = 0.068$, $\eta^2 = 0.030$), and their interaction was significant ($F(1.487, 25.281) = 8.742$, $p = 0.003$, $\eta^2 = 0.090$). Furthermore, simple effect analysis showed that the AM in the CS condition was significantly larger than that in the CL condition ($p < 0.001$, Cohen's $d = 1.627$), and the AM in the AS condition was significantly larger than that in the AL condition ($p = 0.002$, Cohen's $d = 0.891$). However, there was no significant AM difference between HS and HL conditions ($p = 0.147$, Cohen's $d = 0.358$). These results suggest that the tactile duration adaptation resulted in the tactile duration aftereffect, which is dependent on the topographic distance between fingers.

2.2. EEG results

The tactile test stimulus evoked clearly identifiable CNVs both in the fronto-central and contralateral scalps (Fig. 3). Moreover, we observed a clear LPC after the offset of the test stimulus in the fronto-central scalp. Therefore, further statistical analyses were focused on the CNV amplitudes in the fronto-central and contralateral scalps, and LPC amplitude in the fronto-central scalp. Global Field Power (GFP) was used to identify measurement windows (Fig. 3A); this was calculated as the standard deviation of the electrical potential of all electrodes at each time point, resulting in a single value at each time sample (Lehmann and Skrandies, 1980; Murray et al., 2008), and has been used previously to identify the ERP's time-window during temporal perception (Ng et al., 2011; Wiener et al., 2012). Using the GFP from the data for all trials, a "late" (364–608 ms) ERP response was identified after the onset of the tactile test stimulus, which encompassed the CNV in the fronto-central and contralateral scalps (Fig. 3B and D). A peak of GFP activity around 120–280 ms after the offset of the tactile test stimulus was also identified. This time-window encompassed an LPC in the fronto-central scalp (Fig. 3B). Correspondingly, the CNV amplitude was defined as the mean voltage in the 364–608 ms time segment after the onset of the tactile test stimulus in the fronto-central and contralateral scalps. The LPC amplitude was quantified as the mean voltage in a 100 ms window (±50 ms) around the peak of the LPC, which was defined as the maximum value in the 120–280 ms time segment after the offset of the tactile test stimulus in the fronto-central scalp. Similarly to the behavioral results, AMs of the CNV (or LPC) were defined as the arithmetic difference between CNV (or LPC) amplitudes in each adaptation condition and in the no-adaptation condition.

2.2.1. CNV

The duration adaptation effect on the subsequent tactile duration perception in the AM of the CNV was examined using a 2 (scalp location: fronto-central, contralateral) × 2 (adapting duration: short, long) × 3 (adapting location: consistent, adjacent, homologous) repeated-measures ANOVA. This yielded a significant main effect of the adapting location ($F(2, 34) = 9.561$, $p = 0.001$, $\eta^2 = 0.047$), and a significant scalp location × adapting duration interaction ($F(1, 17) = 7.273$, $p = 0.015$, $\eta^2 = 0.054$), and a marginally significant scalp location × adapting location interaction ($F(2, 34) = 3.253$, $p = 0.051$, $\eta^2 = 0.017$). Moreover, a significant scalp location × adapting duration × adapting location interaction ($F(1.493, 25.382) = 3.815$, $p = 0.047$, $\eta^2 = 0.029$) was also observed. To dissect these interactions, separate 2 (adapting duration: short, long) × 3 (adapting location: consistent, adjacent, homologous) repeated-measures ANOVAs were conducted for each scalp location.

In the fronto-central scalp (Fig. 4, left column), a significant main effect of the adapting location was found ($F(2, 34) = 7.296$, $p = 0.002$, $\eta^2 = 0.103$), while no other main effect and interaction were significant (both $ps > 0.05$) (Fig. 5A). Bonferroni post-hoc analyses revealed that
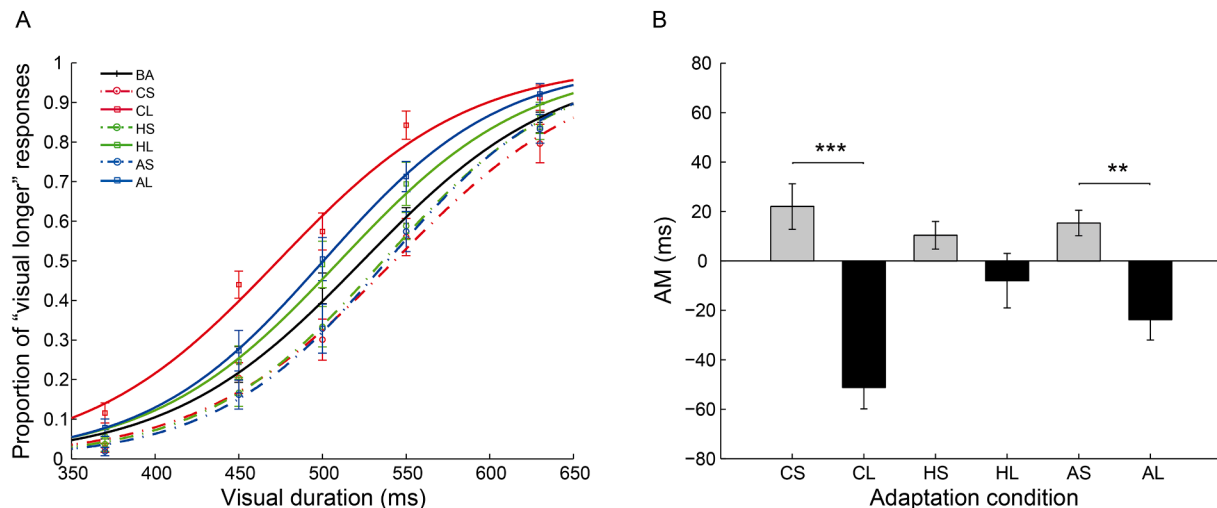
Fig. 2. Results of the behavioral analysis. (A) Psychometric functions (averaged across eighteen participants) showing the proportion of "longer" responses to the visual reference stimuli, which was fitted with a binomial logit function of the visual reference duration in each condition (BA: baseline, no-adaptation; CS, HS, AS: adapt to a short duration on the consistent, homologous, and adjacent fingers, respectively; CL, HL, AL: adapt to a long duration on the consistent, homologous, and adjacent fingers, respectively). (B) AMs of the PSE were calculated as the arithmetic difference between PSEs in each adaptation condition and in the no-adaptation condition. Error bars represent standard errors in each condition. ** $p < 0.01$, *** $p < 0.001$.
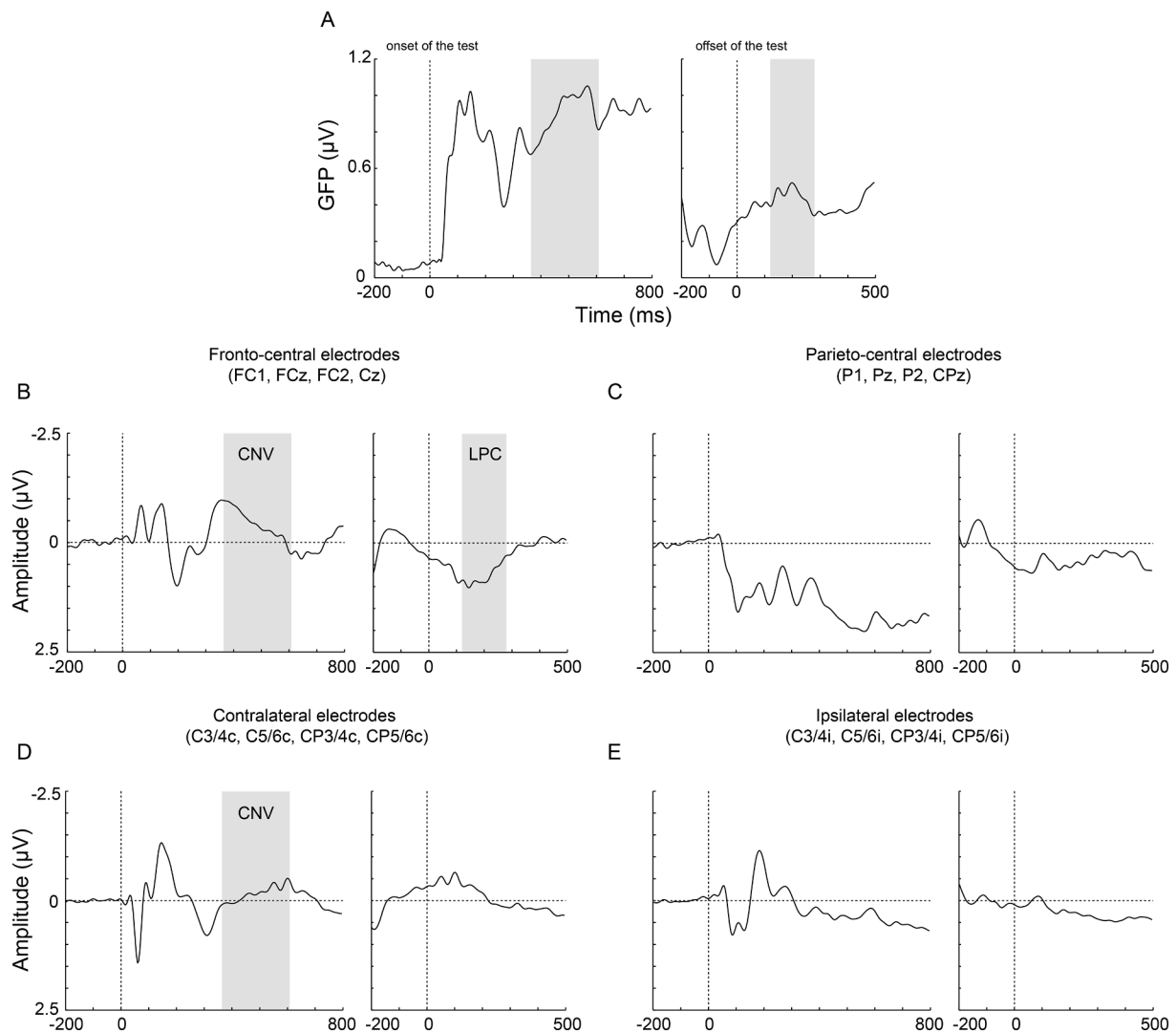
Fig. 3. Measurements of GFP of the group-average ERPs for the onset-lock activity and the offset-lock activity (A) and grand-averaged ERPs displayed between −200 and 800 ms around the tactile test stimulus onset and between −200 and 500 ms around the tactile test stimulus offset, recorded at the fronto-central (B), parieto-central (C), contralateral (D), and ipsilateral (E) electrodes (averaged across all the conditions). The GFP was calculated as the standard deviation of the electrical potential of all electrodes at each time point. The shaded areas represent the measurement windows of CNV and LPC.

the AM in the consistent condition was significantly smaller than that in the adjacent condition ($p = 0.006$, Cohen's $d = -0.851$), and was marginally significantly smaller than that in the homologous condition ($p = 0.067$, Cohen's $d = -0.592$), whereas there was no significant AM difference between homologous and adjacent conditions ($p = 0.508$, Cohen's $d = -0.338$). Based on visual inspection of averaged waveforms, the selected window (364–608 ms) was found to mainly involve the descending part of the CNV. The CNV amplitude (defined as the mean voltage in the 300–608 ms time segment) was thus reanalyzed, but without any change in the results. These results suggest that it is the adapting location, but not the adapting duration, that affects CNV amplitude in the fronto-central scalp.

In the contralateral scalp (Fig. 4, middle column), a significant main effect of the adapting duration ($F(1, 17) = 7.636, p = 0.013, \eta^2 = 0.208$) and a significant interaction ($F(2, 34) = 3.845, p = 0.031, \eta^2 = 0.034$) were found, while the main effect of the adapting location was found to be not significant ($p > 0.05$). Simple effect analysis showed that the AM in the "adapting short" condition was significantly smaller than that in the "adapting long" condition when the adapting location was consistent (CS vs. CL: $p = 0.006$, Cohen's $d = -0.733$) or adjacent (AS vs. AL: $p = 0.031$, Cohen's $d = -0.556$), but not homologous (HS vs. HL: $p = 0.136$,

Cohen's $d = -0.369$) (Fig. 5B). These analyses show that tactile duration adaptation affects the CNV amplitude in the contralateral scalp, which was modulated by the topographic distance between the adapting and test fingers. To further investigate whether changes in CNV amplitude predict the behavioral duration aftereffect at individual level, we analyzed the correlations between the behavioral AM (the arithmetic difference between PSEs in "adapting short" and "adapting long" conditions) and the CNV AM (the arithmetic difference between CNV amplitudes in "adapting short" and "adapting long" conditions) in different adapting location conditions, separately. However, we did not find any significant correlations (all $ps > 0.05$, Fig. S2A), which suggests that the changes in CNV amplitude cannot directly predict the behavioral duration aftereffect.

2.2.2. LPC

We performed a 2 (adapting duration: short, long) × 3 (adapting location: consistent, adjacent, homologous) repeated-measures ANOVA on AMs of the LPC in the fronto-central scalp (Fig. 4, right column). A significant main effect of the adapting duration ($F(1, 17) = 22.080, p < 0.001, \eta^2 = 0.164$) was found. Meanwhile, the main effect of the adapting location ($F(2, 34) = 3.166, p = 0.055, \eta^2 = 0.034$) and the
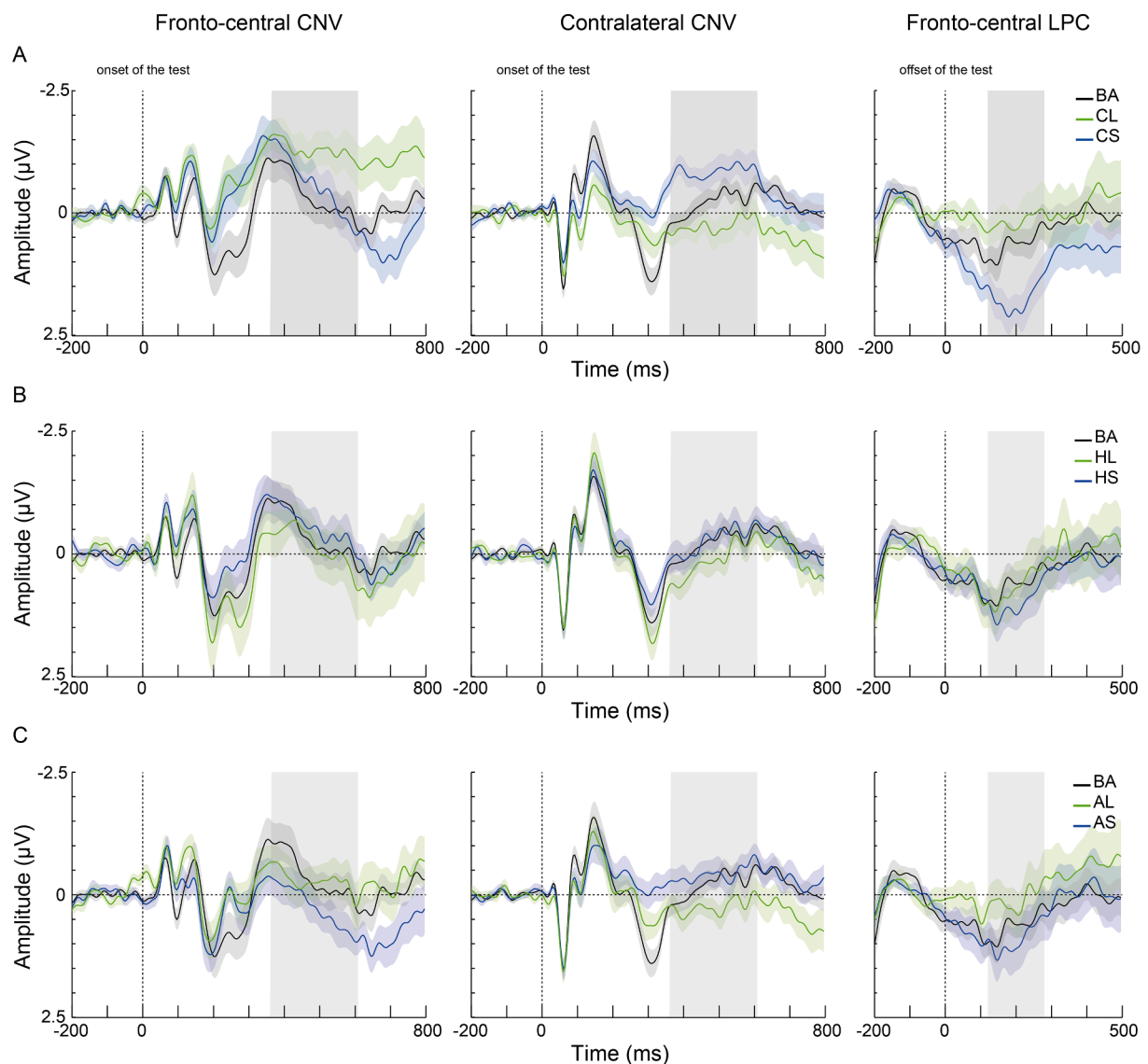
Fig. 4. The CNVs of the fronto-central and contralateral scalps, and the LPCs of the fronto-central scalp in different conditions (BA: baseline, no-adaptation; CS, HS, AS: adapt to a short duration on the consistent, homologous, and adjacent fingers, respectively; CL, HL, AL: adapt to a long duration on the consistent, homologous, and adjacent fingers, respectively). The shadow along each ERP waveform represents the standard errors in each condition and the vertical shadows represent the measurement windows of CNV and LPC.

interaction ($F(2, 34) = 2.692$, $p = 0.082$, $\eta^2 = 0.068$) were found to be marginally significant. Simple effect analysis showed that the AM in the CS condition was significantly larger than that in the CL condition ($p = 0.002$, Cohen's $d = 0.888$), and the AM in the AS condition was significantly larger than that in the AL condition ($p = 0.031$, Cohen's $d = 0.553$), while there was no AM difference between HS and HL conditions ($p = 0.592$, Cohen's $d = 0.129$) (Fig. 5C). The peak latency of the LPC was also analyzed. However, no main effects or interaction were found to be significant (all $ps > 0.05$). These analyses suggest that the LPC amplitude in the fronto-central scalp was modulated by the tactile duration adaptation, which was dependent on the topographic distance between the adapting and test fingers. However, we did not find any significant correlations between the behavioral AM and the LPC AM (the arithmetic difference between LPC amplitudes in "adapting short" and "adapting long" conditions) at individual level in different adapting location conditions, separately (all $ps > 0.05$, Fig. S2B). It suggests that the LPC AM cannot directly predict the behavioral duration aftereffect.

3. Discussion

The present study investigated the effect of tactile duration adaptation on EEG correlates of subsequent tactile duration perception, yielding a number of key findings. First, the tactile duration adaptation induced a significant tactile duration aftereffect when the adapting and test fingers were consistent or adjacent, but not homologous. Second, the tactile duration adaptation has effects on subsequent ERPs: the CNV and LPC amplitudes were found to be strongly modulated by the duration adaptation. Critically, these adaptation effects were dependent on the adapting location. This study hence revealed a coherent behavioral-electrophysiological link for the somatotopically organized tactile duration aftereffect.

Consistent with our previous study (Li et al., 2019), behavioral results provided further evidence that the effect size of the tactile duration aftereffect is contingent on the topographic distance between fingers. Specifically, the aftereffect could transfer to adjacent fingers (even when the frequency of the tactile stimulus was relatively low, i.e., 30 Hz, see Fig. S1B), but not homologous fingers. Moreover, it was found that the
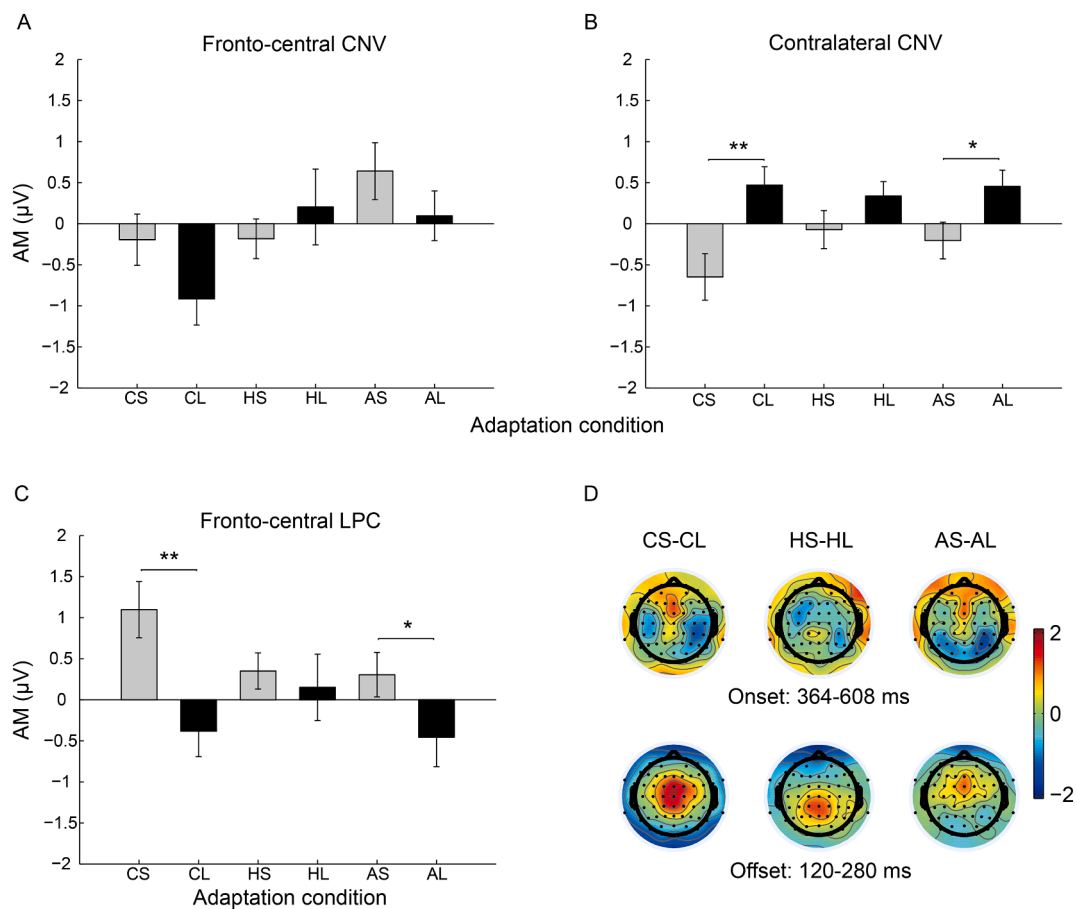
Fig. 5. AMs in ERP components, and difference maps for the measurement windows in different conditions (CS, HS, AS: adapt to a short duration on the consistent, homologous, and adjacent fingers, respectively; CL, HL, AL: adapt to a long duration on the consistent, homologous, and adjacent fingers, respectively). (A) AMs of the CNV in the fronto-central scalp. (B) AMs of the CNV in the contralateral scalp. (C) AMs of the LPC in the fronto-central scalp. (D) The difference maps ("adapting short" – "adapting long") for CNV and LPC components (the left of each map: ipsilateral scalp; the right of each map: contralateral scalp). Error bars represent standard errors in each condition. * $p < 0.05$, ** $p < 0.01$.

behavioral AM was significantly larger in the consistent condition than in the adjacent and homologous conditions (both $ps < 0.01$, Cohen's $ds > 0.700$). There was a marginally significant difference for behavioral AMs between adjacent and homologous conditions ($p = 0.079$, Cohen's $d = 0.440$). This result further suggests that the transfer of the tactile duration aftereffect between adjacent fingers is only partial, not full.

Our previous study has demonstrated that the duration aftereffect is contingent on the low-level auditory feature (i.e., auditory frequency) but not on the low-level visual feature (i.e., visual orientation) (Li et al., 2015). This suggests the duration adaptation in the auditory modality may arise at a relatively earlier stage of sensory processing than that in the visual modality. Here, similar to the auditory duration aftereffect, the tactile duration aftereffect is dependent on the topographic distance between fingers. This is consistent with the characteristics of early stages of tactile processing (Burton and Sinclair, 1996), and suggests an early duration adaptation mechanism in the somatosensory system. The early adaptation mechanism is also consistent with previous studies on the frequency adaptation (Murai et al., 2016). For example, the temporal-compression aftereffect, resulting from adaptation to dynamic stimuli (e.g., visual motion or flicker, tactile flutter), has been found in the visual and tactile modalities (Johnston et al., 2006; Watanabe et al., 2010). This aftereffect is spatially specific, and limited to relatively high temporal frequencies, which suggests the pre-cortical processing of duration (Ayhan et al., 2009; Bruno et al., 2010; Johnston et al., 2006; Watanabe et al., 2010). However, the tactile duration aftereffect observed here partially transferred to the adjacent fingers, and was independent of the frequency of the tactile stimulus (see the supplement,

Fig. S1B). These results suggest the tactile duration aftereffect should not result from the adaptation of tactile response channels (mechanoreceptive afferents), and imply a cortical processing of duration in the somatosensory cortex.

To further uncover how the tactile duration adaptation modulates subsequent perception of tactile duration, this study focused on the CNV evoked by the onset of the tactile test stimulus – the point at which temporal encoding is engaged – and also on the LPC evoked by the offset of the tactile test stimulus during the temporal memory stage. Adaptation to the shorter tactile duration was found to increase the CNV amplitude (in the contralateral scalp) whereas adaptation to the longer tactile duration decreased it. A similar modulation was observed in the LPC amplitude in the fronto-central scalp. Importantly, those modulations took place only when the adapting and test stimuli were presented on consistent or adjacent fingers, but not homologous fingers. These ERP results match well with the observations from behavioral results. Since previous studies have suggested that the CNV amplitude reflects the neural correlates of temporal encoding (Macar et al., 1999; Wiener et al., 2012), these CNV results suggest that the tactile duration adaptation modulates subsequent temporal encoding. It is also consistent with a previous study on the visual duration aftereffect (Li et al., 2017). In addition, the LPC observed here was similar to the P150 evoked in the central scalp at the offset of the comparison interval for a short interval as reported by Tarantino et al. (2010). It has been suggested that the P150 is related to working memory processes. Accordingly, these results further indicate that the later temporal processing mechanism (i.e., temporal memory) is also involved in the tactile duration aftereffect.

Previous studies demonstrated that the CNV is typically found over the fronto-central scalp during explicit temporal processing (Kononowicz and van Rijn, 2014; Li et al., 2017; Wiener et al., 2012). In this study, CNVs were observed not only in the fronto-central scalp, but also in the contralateral scalp. This is consistent with a previous finding that showed the CNV is widespread across the scalp (Pfeuty et al., 2008). However, this study found that only the CNV in the contralateral scalp is sensitive to the duration adaptation effect. This dissociative pattern suggests that CNVs in the fronto-central and contralateral scalps might reflect different temporal processes, such as accommodating to specific tasks such as explicit vs. implicit timing. Indeed, a recent study found that the time interval adaptation has no effect on the CNV amplitude in the fronto-central scalp when participants were asked to complete an implicit timing task (Kaya et al., 2017). In addition, Praamstra et al. (2006) investigated the neurophysiology of implicit timing and found that CNV manifestations of implicit timing originate in the lateral instead of the medial premotor cortex.

The adaptation effect on the CNV in the contralateral scalp is consistent with the inference of the behavioral result, which suggests the early somatosensory areas play an essential role in the sub-second tactile duration perception. This is in line with previous studies, which suggest the primary somatosensory cortex (S1) is involved in tactile temporal processing (Conte et al., 2012; Rocchi et al., 2016). According to the duration channel-based model, our brain contains duration-tuned neurons, each of which responds selectively to a narrow range of stimulus durations centered on its preferred duration (Heron et al., 2012). Consistent with this idea, duration-tuned neurons have been found in the visual and auditory nervous systems in specific animal species (Casseday et al., 1994; Duysens et al., 1996; Faure et al., 2003). Recent fMRI studies also showed that such duration-selective neurons exist in the human right parietal cortex, in which the neuron adaptation is related to the visual duration aftereffect (Hayashi et al., 2015; Hayashi and Ivry, 2020). Combined with the present results, it is possible that the duration-tuned neurons also exist in the somatosensory system. However, little evidence has suggested the direct relation between the response of duration-tuned neurons and the CNV activity. Instead, it has suggested that the CNV could be driven by a climbing neural activity process (Pfeuty et al., 2005; Reutimann et al., 2004). Therefore, the CNV in the contralateral scalp might not directly reflect the overall activity of duration-tuned neurons in the early somatosensory areas. Instead, it is possible that other neurons which receive the signals from the duration-tuned neurons may generate the CNV.

There is an ongoing debate on the perceptual and cognitive functions underlying the ERP component of CNV (Kononowicz and Penney, 2016; van Rijn et al., 2011). Previous studies have focused on CNV activity during a temporal comparison task, in which participants compared a current duration to a memorized duration and then prepared a motor response (Macar and Vidal, 2003; Ng et al., 2011; Pfeuty et al., 2003). As such, the CNV evoked during temporal comparison may reflect multiple cognitive processes, including memory encoding and subsequent decision making. In the present study, the tactile test stimulus was always presented before the visual reference stimulus, and participants made their responses after the visual reference stimulus. This made it possible to investigate the adaptation effect on the subsequent CNV evoked by the onset of the tactile test stimulus, largely free from memory, motor preparation, and decision processes. Moreover, this manipulation also helped to distinguish the LPC evoked by the offset of the tactile test stimulus from the LPCt related to decision-making that was observed in previous studies (Paul et al., 2003, 2011). However, it should be noted that presenting the tactile test stimulus before the visual reference stimulus also simplified the duration discrimination task. In this situation, participants may pay more attention to the visual reference with variable durations, and timing for the tactile test stimulus could be more implicit. To some extent, this design could explain why the duration adaptation effect on the CNV amplitude in the fronto-central scalp was not observed.

In the present study, the adaptation effect on typical somatosensory components (e.g., P45, N80, P100, N140, Nd1) was not examined. Identical numbers of adapting stimuli were used in all adaptation tests, and this means that the total period of the tactile adaptation was different between "adapting long" and "adapting short" conditions. It has been suggested that the tactile adaptation itself could affect these earlier somatosensory components (Bradley et al., 2014). Therefore, it was not possible to strictly distinguish the effects of the duration adaptation vs. the tactile adaptation on these components. Nevertheless, this does not mean that the tactile duration adaptation has no effect on these components. An important avenue for future research would be to examine the duration adaptation effect on these earlier somatosensory components by controlling the total duration of adapting stimuli (e.g., adapting to the unfilled interval marked by two brief tactile stimuli). Accordingly, one may question whether the effects of the duration adaptation on the CNV and LPC amplitudes were merely the result of the total period of adaptation. We found that the AM of the CNV in the contralateral scalp and the AM of the LPC in the fronto-central scalp were dependent on the duration of the adapting stimulus, but not on the tactile adaptation itself. This is not consistent with the hypothesis that the tactile adaptation itself could modulate subsequent CNV and LPC amplitudes. To further rule out this possibility, a supplementary analysis was conducted, in which the ERPs between no-adaptation and adaptation conditions were compared regardless of adapting durations (Fig. S3). The results showed that there was no significant difference for either CNV or LPC amplitudes between the adaptation and no-adaptation conditions (both $ps > 0.05$). Thus, it was the tactile duration adaptation, and not merely the tactile adaptation, that modulated subsequent CNV and LPC amplitudes.

Although we found significant effects of the tactile duration adaptation on CNV and LPC amplitudes, the changes of the two ERP components cannot directly predict the behavioral duration aftereffect at individual level. The underlying reasons may be complicated. One possibility is that the duration judgement in the present duration discrimination task was determined not only by the tactile test stimulus, but also by the subsequent visual reference stimulus. Thus, the temporal processing for the tactile stimulus alone could not predict the overall outcome of the duration judgement.

In sum, the present study used EEG to investigate how the tactile duration adaptation affects subsequent tactile duration perception. It provides further evidence that the tactile duration adaptation results in the tactile duration aftereffect, which is organized within a somatotopic framework. Moreover, this adaptation effect is manifested in the CNV and LPC amplitudes, which are respectively associated with temporal encoding and memory processes. In the information processing perspective, this indicates that the tactile duration adaptation not only modulates subsequent temporal encoding, but also modulates subsequent temporal memory. The present study helps us to understand the neural underpinnings of the tactile duration aftereffect.

4. Experimental procedures

4.1. Participants

Twenty-two healthy participants were recruited. All participants reported normal or corrected-to-normal vision and normal tactile sensations and had no history of neurological diseases. They were naïve to the purpose of the experiment. They gave written informed consent and were paid for their time. The study was conducted in accordance with the principles of the Declaration of Helsinki and was approved by the human subject review committee of Peking University. Data from four participants were discarded, due to their poor performance in the duration discrimination task or excessive artifacts in the EEG data. The final sample was composed of eighteen participants (9 females; mean age: 20.28 ± 1.49 years).

4.2. Apparatus and stimuli

Participants were comfortably seated in a chair in a dim, sound-attenuated, and temperature-controlled room. The visual stimulus was a white disk (2.8° in diameter), which was presented on the center of a CRT monitor (100 Hz refresh rate, 1024 × 768 pixels) with a gray background. The tactile stimulus was a sine-wave vibration (150 Hz) characterized by a 5-ms cosine on- and off-ramp. The vibration was delivered to a round aluminum probe (6.0 mm in diameter) by a piezo-tactile stimulator (Dancer Design, St Helens, Merseyside, England), which was connected to a digital-to-analog conversion sound card. The probe was located in a hole (8.0 mm in diameter) in one end of a rect-angular machined ceramic case. During the experiment, participants placed their fingers against the cases and touched the flat surfaces of the probes with their fingertips. Finger rests were used to fix the contact position between the finger and the probe (Fig. 1). Participants wore headphones (with continuously presented pink noise) and earplugs to maximally shield the noise from the vibrating stimulator. Participants' hands were covered by an opaque towel and hence invisible throughout the experiment. Stimulus presentation and behavioral data collection were implemented with Matlab (Mathworks Inc.) and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

4.3. Procedure

During the experiment, participants completed experimental tasks with eight blocks: two no-adaptation blocks and six adaptation blocks. In each no-adaptation block, participants put their hands with palm downward on the supporting desk and kept their eyes on the center of the screen. During each trial, a test and a reference were presented successively with an inter-stimulus interval (ISI) of 1000–1500 ms. The test was a 500-ms tactile stimulus presented on the index fingertip of the left or right (counterbalanced across participants) hand. Given that our pilot experiment showed that the tactile duration aftereffect did not transfer to the visual modality (see the supplement, Fig. S1A), we used the visual stimulus as the reference, whose duration was one of five durations: 370 ms, 450 ms, 500 ms, 550 ms, 630 ms. These reference durations were presented randomly but counterbalanced. Upon the disappearance of the reference, participants made an unspeeded, two-alternative forced-choice (2AFC) to determine which stimulus (tactile or visual) lasted longer. Participants pressed the left or right mouse button with their thumbs to indicate their responses. The button press was counterbalanced across participants: half the participants pressed the left button for "tactile longer" and the right button for "visual longer", while the other half responded with the reversed mapping. There were 60 trials in each no-adaptation block, with 12 trials for each reference duration.

Each adaptation block included two phases: adaptation and test. During the adaptation phase, an adapting tactile stimulus with a brief duration (200 or 800 ms) was repeatedly presented 80 times, with an ISI of 500–1000 ms. After this initial adaptation phase, a test phase followed. The test phase was similar to the no-adaptation block, except that four top-up stimuli, which were identical to those presented in the preceding adaptation phase, were presented before each test stimulus. The interval between the last top-up stimulus and the test was 1500–2500 ms.

The different combinations of fingers and durations used in the adaptation phase resulted in six adaptation blocks: "adapt to a short duration on the consistent finger (CS)", "adapt to a long duration on the consistent finger (CL)", "adapt to a short duration on the homologous finger (HS)", "adapt to a long duration on the homologous finger (HL)", "adapt to a short duration on the adjacent finger (AS)", and "adapt to a long duration on the adjacent finger (AL)". The test stimulus was presented on the index finger of the left (or right) hand, and thus the "consistent", "homologous" and "adjacent" fingers respectively referred to the index finger of the left (or right) hand, the index finger of the right

(or left) hand, and the middle finger of the left (or right) hand (Fig. 6). In homologous and adjacent conditions, the physical distance between the adapting and test fingertips was about 4 cm. In the experiment, the order of adaptation blocks was random. Two no-adaptation blocks were given before and after the adaptation blocks, respectively. After each block, participants took a break of at least two minutes to wash out any potential carry-over effect between blocks.

4.4. EEG recording and analysis

Continuous EEG was recorded from 64 Ag/AgCl electrodes according to the extended international 10–20 system (Brain Products GmbH, Steingrabenstr, Germany). An electrooculogram (EOG) was simultaneously recorded using one electrode located below the right eye. Data were sampled at 500 Hz with an online 0.016–250 Hz band-pass filter. Electrode impedances were kept below 5 kΩ.

Offline EEG data were preprocessed using EEGLAB for Matlab (Delorme and Makeig, 2004). Recordings were first re-referenced to the average voltage of all scalp electrodes and down-sampled to 250 Hz. A low-pass-filter was then applied at 30 Hz via a conventional finite impulse response (FIR) filter. The continuous EEG data were epoched from −200 to 1000 ms relative to the 500-ms tactile test stimulus onset. All epochs were baseline-corrected with a 200-ms pre-stimulus window. All epochs were visually examined and trials containing large EEG artifacts were thereby discarded. Remaining eye movement artifacts were removed via independent component analysis (ICA), according to the participant's scalp maps and activity profile (Jung et al., 2000). Lastly, epochs containing voltage deviations exceeding ±100 µV at any of the recording electrodes were rejected. With this preprocessing procedure, on average, 113 (94% of total) trials were included for further analysis in the no-adaptation condition and 56 (93% of total) trials remained per adaptation condition for each participant. Moreover, a 2 (adapting duration: short, long) × 3 (adapting location: consistent, adjacent, homologous) repeated-measures analysis of variance (ANOVA) showed that the numbers of remaining trials were balanced across different adaptation conditions. Both main effects of the numbers of sorted trials according to the adapting duration and the adapting location and their interaction were found to be not significant (all $ps > 0.05$). To better define ERPs related to specific events, the EEG signal was further segmented according to the onset and offset of the tactile test stimulus. That is, two types of epoch were extracted: (1) an epoch ranging from −200 to 800 ms relative to the onset of the tactile test stimulus (with a baseline of the 200 ms interval preceding the onset); (2) an epoch
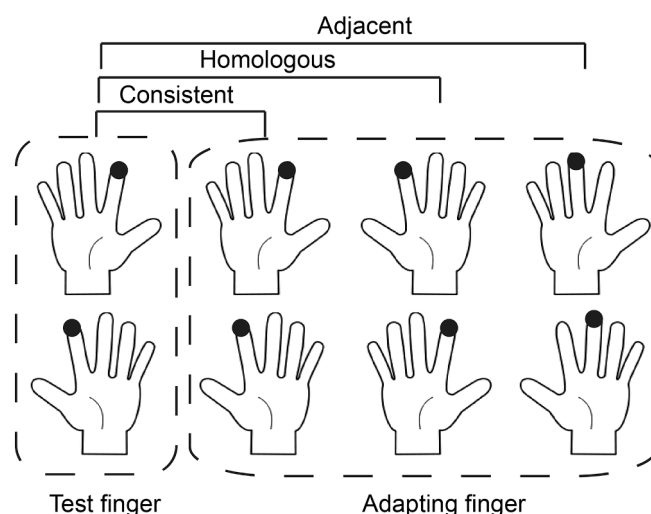

Fig. 6. The schema of test and adapting fingers. The black dots indicate fingers where the tactile stimuli were presented.

ranging from −200 to 500 ms relative to the offset of the tactile test stimulus (with a baseline of the 200 ms interval preceding the offset).

Here, we focused on the fronto-central and parieto-central electrode sites, where the CNV or the post-stimulus components were usually reported to be maximal (Macar and Vidal, 2004; Tarantino et al., 2010). Moreover, given that our previous study has suggested somatosensory areas play an essential role in the tactile time processing (Li et al., 2019), electrodes over the somatosensory cortex were also demonstrated. To increase the signal-to-noise ratio, ERPs were analyzed by pooling four neighboring electrodes within four regions of interest on a scalp level (scalp-ROIs). Four cohorts of scalp-ROIs were distributed in the fronto-central scalp (Cz, FC1, FCz, FC2), parieto-central scalp (P1, Pz, P2, CPz), and contralateral/ipsilateral scalps (C3/4, C5/6, CP3/4, CP5/6).

CRediT authorship contribution statement

Baolin Li: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Jianrong Jia:** Methodology, Investigation, Writing - review & editing. **Lihan Chen:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **Fang Fang:** Conceptualization, Methodology, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.brainres.2021.147432.

References

Ayhan, I., Bruno, A., Nishida, S., Johnston, A., 2009. The spatial tuning of adaptation-based time compression. J. Vis. 9, 1–12.

Bendixen, A., Grimm, S., Schröger, E., 2005. Human auditory event-related potentials predict duration judgments. Neurosci. Lett. 383, 284–288.

Bradley, C., Joyce, N., Garcia-Larrea, L., 2014. Adaptation in human somatosensory cortex as a model of sensory memory construction: a study using high-density EEG. Brain Struct. Funct. 221, 421–431.

Brainard, D.H., 1997. The psychophysics toolbox. Spat. Vis. 10, 433–436.

Bruno, A., Ayhan, I., Johnston, A., 2010. Retinotopic adaptation-based visual duration compression. J. Vis. 10, 1–18.

Burr, D., Tozzi, A., Morrone, M.C., 2007. Neural mechanisms for timing visual events are spatially selective in real-world coordinates. Nat. Neurosci. 10, 423–425.

Burton, H., Sinclair, R., 1996. Somatosensory cortex and tactile perceptions. In: Kruger, L. (Ed.), Pain and Touch. Academic Press, San Diego, pp. 105–177.

Casseday, J., Ehrlich, D., Covey, E., 1994. Neural tuning for sound duration: role of inhibitory mechanisms in the inferior colliculus. Science 264, 847–850.

Conte, A., Rocchi, L., Nardella, A., Dispenza, S., Scontrini, A., Khan, N., Berardelli, A., 2012. Theta-burst stimulation-induced plasticity over primary somatosensory cortex changes somatosensory temporal discrimination in healthy humans. PLoS ONE 7, e32979.

Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J. Neurosci. Methods 134, 9–21.

Duysens, J., Schaafsma, S., Orban, G., 1996. Cortical off response tuning for stimulus duration. Vision Res. 36, 3243–3251.

Faure, P.A., Fremouw, T., Casseday, J.H., Covey, E., 2003. Temporal masking reveals properties of sound-evoked inhibition in duration-tuned neurons of the inferior colliculus. J. Neurosci. 23, 3052–3065.

Fujisaki, W., Shimojo, S., Kashino, M., Nishida, S., 2004. Recalibration of audiovisual simultaneity. Nat. Neurosci. 7, 773–778.

Gibbon, J., 1977. Scalar expectancy theory and Weber's law in animal timing. Psychol. Rev. 84, 279–325.

Hayashi, M.J., Ditye, T., Harada, T., Hashiguchi, M., Sadato, N., Carlson, S., Walsh, V., Kanai, R., 2015. Time adaptation shows duration selectivity in the human parietal cortex. PLoS Biol. 13, e1002262.

Hayashi, M.J., Ivry, R.B., 2020. Duration selectivity in right parietal cortex reflects the subjective experience of time. J. Neurosci. 40, 7749–7758.

Herbst, S.K., Chaumon, M., Penney, T.B., Busch, N.A., 2014. Flicker-induced time dilation does not modulate EEG correlates of temporal encoding. Brain Topogr. 28, 559–569.

Heron, J., Aaen-Stockdale, C., Hotchkiss, J., Roach, N.W., McGraw, P.V., Whitaker, D., 2012. Duration channels mediate human time perception. Proc. R. Soc. B-Biol. Sci. 279, 690–698.

Johnston, A., Arnold, D.H., Nishida, S., 2006. Spatially localized distortions of event time. Curr. Biol. 16, 472–479.

Jung, T.-P., Makeig, S., Westerfield, M., Townsend, J., Courchesne, E., Sejnowski, T.J., 2000. Removal of eye activity artifacts from visual event-related potentials in normal and clinical subjects. Clin. Neurophysiol. 111, 1745–1758.

Kaya, U., Yildirim, F.Z., Kafaligonul, H., 2017. The involvement of centralized and distributed processes in sub-second time interval adaptation: an ERP investigation of apparent motion. Eur. J. Neurosci. 46, 2325–2338.

Kononowicz, T.W., Penney, T.B., 2016. The contingent negative variation (CNV): timing isn't everything. Curr. Opin. Behav. Sci. 8, 231–237.

Kononowicz, T.W., van Rijn, H., 2014. Decoupling interval timing and climbing neural activity: a dissociation between CNV and N1P2 amplitudes. J. Neurosci. 34, 2931–2939.

Lehmann, D., Skrandies, W., 1980. Reference-free identification of components of checkerboard-evoked multichannel potential fields. Electroencephalogr. Clin. Neurophysiol. 48, 609–621.

Li, B., Chen, L., Fang, F., 2019. Somatotopic representation of tactile duration: evidence from tactile duration aftereffect. Behav. Brain Res. 371, 111954.

Li, B., Chen, Y., Xiao, L., Liu, P., Huang, X., 2017. Duration adaptation modulates EEG correlates of subsequent temporal encoding. Neuroimage 147, 143–151.

Li, B., Yuan, X., Huang, X., 2015. The aftereffect of perceived duration is contingent on auditory frequency but not visual orientation. Sci. Rep. 5, 10124.

Lindbergh, C.A., Kieffaber, P.D., 2013. The neural correlates of temporal judgments in the duration bisection task. Neuropsychologia 51, 191–196.

Macar, F., Vidal, F., 2003. The CNV peak: an index of decision making and temporal memory. Psychophysiology 40, 950–954.

Macar, F., Vidal, F., 2004. Event-related potentials as indices of time processing: a review. J. Psychophysiol. 18, 89–104.

Macar, F., Vidal, F., Casini, L., 1999. The supplementary motor area in motor and sensory timing: evidence from slow brain potential changes. Exp. Brain Res. 125, 271–280.

Murai, Y., Whitaker, D., Yotsumoto, Y., 2016. The centralized and distributed nature of adaptation-induced misjudgments of time. Curr. Opin. Behav. Sci. 8, 117–123.

Murray, M.M., Brunet, D., Michel, C.M., 2008. Topographic ERP analyses: a step-by-step tutorial review. Brain Topogr. 20, 249–264.

Nagai, Y., Critchley, H.D., Featherstone, E., Fenwick, P.B., Trimble, M.R., Dolan, R.J., 2004. Brain activity relating to the contingent negative variation: an fMRI investigation. Neuroimage 21, 1232–1241.

Ng, K.K., Penney, T.B., 2014. Probing interval timing with scalp-recorded electroencephalography (EEG). Adv. Exp. Med. Biol. 829, 187–207.

Ng, K.K., Tobin, S., Penney, T.B., 2011. Temporal accumulation and decision processes in the duration bisection task revealed by contingent negative variation. Front. Integr. Neurosci. 5, 77.

Paul, I., Le Dantec, C., Bernard, C., Lalonde, R., Rebaï, M., 2003. Event-related potentials in the frontal lobe during performance of a visual duration discrimination task. J. Clin. Neurophysiol. 20, 351–360.

Paul, I., Wearden, J., Bannier, D., Gontier, E., Dantec, C.L., Rebaï, M., 2011. Making decisions about time: event-related potentials and judgements about the equality of durations. Biol. Psychol. 88, 94–103.

Pelli, D.G., 1997. The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat. Vis. 10, 437–442.

Pfeuty, M., Ragot, R., Pouthas, V., 2003. When time is up: CNV time course differentiates the roles of the hemispheres in the discrimination of short tone durations. Exp. Brain Res. 151, 372–379.

Pfeuty, M., Ragot, R., Pouthas, V., 2005. Relationship between CNV and timing of an upcoming event. Neurosci. Lett. 382, 106–111.

Pfeuty, M., Ragot, R., Pouthas, V., 2008. Brain activity during interval timing depends on sensory structure. Brain Res. 1204, 112–117.

Praamstra, P., Kourtis, D., Kwok, H.F., Oostenveld, R., 2006. Neurophysiology of implicit timing in serial choice reaction-time performance. J. Neurosci. 26, 5448–5455.

Reutimann, J., Yakovlev, V., Fusi, S., Senn, W., 2004. Climbing neuronal activity as an event-based cortical representation of time. J. Neurosci. 24, 3295–3303.

Rocchi, L., Casula, E., Tocco, P., Berardelli, A., Rothwell, J., 2016. Somatosensory temporal discrimination threshold involves inhibitory mechanisms in the primary somatosensory area. J. Neurosci. 36, 325–335.

Tarantino, V., Ehlis, A.-C., Baehne, C., Boreatti-Huemmer, A., Jacob, C., Bisiacchi, P., Fallgatter, A.J., 2010. The time course of temporal discrimination: an ERP study. Clin. Neurophysiol. 121, 43–52.

Treisman, M., 1963. Temporal discrimination and the indifference interval: implications for a model of the "internal clock". Psychol. Monogr. 77, 1–31.

van Rijn, H., Kononowicz, T.W., Meck, W.H., Ng, K.K., Penney, T.B., 2011. Contingent negative variation and its relation to time estimation: a theoretical evaluation. Front. Integr. Neurosci. 5, 91.

Walker, J.T., Irion, A.L., Gordon, D.G., 1981. Simple and contingent aftereffects of perceived duration in vision and audition. Percept. Psychophys. 29, 475–486.

Watanabe, J., Amemiya, T., Nishida, S., Johnston, A., 2010. Tactile duration compression by vibrotactile adaptation. NeuroReport 21, 856–860.

Wiener, M., Kliot, D., Turkeltaub, P.E., Hamilton, R.H., Wolk, D.A., Coslett, H.B., 2012. Parietal influence on temporal encoding indexed by simultaneous transcranial magnetic stimulation and electroencephalography. J. Neurosci. 32, 12258–12267.